JUGLANS HINDSII, THE CENTRAL CALIFORNIA BLACK WALNUT, NATIVE OR INTRODUCED?

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Many anthropologists have noted that a distinctive vegetation tends to appear on man's habitation sites. Hrdlicka (1945) quoted Eyerdam as stating that the site of stone age villages in the Aleutians could generally be recognized during spring and summer by the predominance of two perennial plants, *Heracleum lanatum* Michx. (wild rhubarb or cow parsnip), and *Aconitum kamtschaticum* Rchb. (monkshood). Lillard, Heizer and Fenenga (1939) state that nettles and thistles were often associated with village sites in the Sacramento Valley. A more recent observation was made by Elsasser (1960) that "mule-ears" (*Wyethia mollis* Gray) sharply defined the extent of a California Indian habitation site in the Sierra foothills.

The association of certain plants and man has an obvious practical use in site reconnaisance; a two-year study made by Zeiner (1946) at the Angel Mounds in Indiana demonstrated that the location of buried walls and earthworks could be traced by the distribution of certain species of plants. Although of less immediate application, it would seem that consideration should also be given to the possibility that a useful chronology might be established on the basis of plant progression. In either case, such study would necessarily involve the differentiation of the plant cover into categories of indigenous and introduced flora.

The investigator into the relationship of vegetation to man's occupation in California would pretty surely turn to the publications of Willis Linn Jepson, whose "A Flora of California," "The Silva of California," and "A Manual of the Flowering Plants of California," have been the primers for several generations of botanists. Jepson (1909, p. 365; 1910, p. 194) made the observation that the central California black walnut was to be found near ancient Indian village sites, although little significance was attached to his observation at the time.

An anthropological study of known Indian sites in the Bay Area counties was initiated in an effort to ascertain if the black walnut is, in fact, a plant associated with pre-contact habitations of the California Indian. In the course of the investigation it became evident that on the basis of present-day evidence, definite proof is lacking as to whether or not the black walnut of central California is indigenous or introduced. The widespread use of black walnut as a rootstock for the commercial propagation of the English walnut (*Juglans regia* L.) has proliferated the occurrence of the black walnut to such an extent that no Indian association with a given stand can be verified or disproved without a determination of its origin.

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The anthropological study is continuing; questions which should still be answered include: were the riparian locations that were so often occupied advantageous to both the trees and to the indigenous peoples, hence the shade and the fruits were utilized fortuitously? Since so good and portable a source of food must have been transported during the seasonal migrations of the Indians, is the presence of walnuts at non-riparian locations the result of accidental seeding by man or by rodents? Or is their location in sites well above permanent water courses the result of natural distribution and an indigenous origin, the present isolated groves of trees representing relictual stands?

In order to attempt an answer to the possibility of natural origin as contrasted to introduction by Indians, the writer was led into a study of the fossil record, with the result that a case is made herein for the distribution of the central California black walnut, *Juglans hindsii* (Jeps.) Jeps., as an indigenous plant of central California.

Six to nine genera are recognized by taxonomists dealing with Juglandaceae; the present investigation will be concerned with three of these: *Carya*, *Pterocarya*, and *Juglans*. Of the three sections in the genus *Juglans* (sections *Rhysocaryon*, *Cardiocaryon* and *Dioscaryon*), the discussion will deal primarily with section *Rhysocaryon*, since all of the western North American species of *Juglans* can be assigned to this section. Wolfe (1959, p. 13) considers that morphologically,

"There are two distinct groups of species in *Rhysocaryon*. One of these groups, including *J. nigra* and the Central and South American species tends to have leaflets which have a broad base and a broadly triangular (ovate) shape. . . . The other group of species have teeth which are broadly triangular and dentate, or narrowly conical and serrate. The shape is narrowly triangular although a narrowly quadrate condition prevails in *J. californica*". Wolfe's work is mainly concerned with foliar characteristics, and minor attention is given to fossil fruits. An essential basis for differentiation between the extant species of *Juglans* which are either introduced or occur naturally in California lies in the fruits. Unlike its eastern cousin, the rugose *J. nigra* L., which has a strongly grooved black shell, or the important commercial so-called English walnut, *J. regia* L., the central California black walnut, *J. hindsii* (Jeps.) Jeps., has a characteristically smooth or very lightly-grooved nut, light brown in color. In shape, the fruits of both *J. nigra* and *J. regia* are characteristically longer and more pointed than in *J. hindsii*. Specimens of *J. hindsii* fruits taken in widely separated parts of the central California habitat show a consistent roundness, with a flattened stem end, reminiscent of the tiny Eocene *J. clarnensis* Scott. Foliar characters differ among the three, especially in the number of leaflets: *J. hindsii* has as many as nineteen leaflets and seldom fewer than fifteen; *J. nigra* may have as many as twenty-seven leaflets, while *J. regia* usually has seven, but sometimes five.

There are two centers of distribution for California black walnuts, one in the southern part of the state and one in the north-central part, the trees occurring without connecting localities. The northern California black walnut was discovered along the lower Sacramento River area by Richard Brinsley Hinds of the Sulphur Expedition in 1837. By an historical accident, however, the black walnut of southern California was described first as *J. californica* by Watson (1875), who included within his concept *J. rupestris* Engl. var. *major* Torr., the walnut of Arizona and Texas. Jepson (1908) named the northern California trees as a variety of the southern ones, *J. californica* var. *hindsii,* honoring their discoverer and saying that the trees of the two regions "differ somewhat."

In his Flora, Jepson (1909) still contented himself with this varietal concept, averring that the northern trees were introduced from southern California by the trading of the native Indian tribes. In his Silva (1910), he continued the same concept but pointed out certain anomalies, namely that (1) Watson's original description of *J. californica* did not cite a type and included as a synonym the walnut of Arizona and Texas, *J. rupestris* var. *major*, and (2) the southern, rather than the northern California walnuts must bear the name *J. californica* Wats. for several reasons: Watson had no northern specimen before him, his northern locality was vague, his description better fitted the southern form. It was not so easy, however, for Jepson to ignore a further anomaly, the peculiar gap in distribution between southern and northern California (275 miles between stations in Ventura County and near Mount Diablo), and he concluded again that the introduction from the south by native tribes was the only plausible explanation for the existence of the northern trees. Later, however, in his Manual (1923) he elevated the northern trees to the rank of a species, without further discussion, as *J. hindsii* (Jeps.) Jeps., a tacit admission that he must have come to the point of view that the original black walnuts of central California, present before the white man arrived, were indigenous and were not introduced from those of southern California. His morphological treatment bears this out.

A review of the paleontological literature of the past half century may give perspective to the facts of distribution of California *Juglans*. Since the fossil beds are distributed in space as well as in time, the discussion of these deposits and their relation to *Juglans* can be more easily followed if they are examined by geographical groupings as well as by geological time periods. A glance at a relief map of the western United States discloses that territorially the area is broken up into clearly defined regions by the Coast, the Cascade and the Sierra Nevada mountain ranges; these ranges run roughly parallel longitudinally. Minor ranges, the Klamath to the northwest, and the Warner to the northeast, complete the California picture. One major transmontane range, the Tehachapi Mountains, shuts off northern from southern California, forming the southern rim of the great Central Valley, whose rivers converge from north, east and south towards San Francisco Bay.

Some paleontological literature has been available since Jepson first became interested in the problem of *Juglans* and its distribution. Sudworth (1908) remarked on the presence of fossil walnut remains in Cretaceous and Tertiary formations, noting that ". . . . in the northern Pacific coast region signs of ancient walnuts have been obtained from the Eocene formation, as well as from the gold-bearing gravel beds of the California Sierra". There follows a brief and very simplified discussion of the subsequent paleontological literature which bears on the subject.

The fossil floras of California, Oregon and Washington indicate tropical conditions for the Eocene, although changes in physiography due to volcanic action and mountain uplift were making for localized climates. Scott (1954) described the fossil fruits and seeds from the Eocene Clarno formation of north-central Oregon. He discussed the similarity of the nuts of *Carya* and *Juglans*, designating the fruits of the Clarno species, *Juglans clarnensis*, and describing them as having features intermediate between those of sections *Cardiocaryon* and *Rhysocaryon*. He says: ". . This is the first certain walnut described from rocks as old as Eocene. This occurrence of *Juglans* demonstrates that the fruits of the walnut and the hickory (*Carya*) were generically distinct during Eocene time". It should be remarked here, however, that Wolfe (1959, p. 43) assigns *J. clarnensis* Scott to the Oligocene.

In the Oligocene, tropical fauna were still ranging up to Puget Sound, and the fossil flora of southern Alaska indicates a warm, temperate zone at that latitude (Smith, 1919). In other parts of North America, such as in North Dakota and Colorado, fossil beds containing *Juglans* material have been related to Oligocene time, and Wolfe (1959, p. 46) places *J. kentensis*, from a bed in northwest Oregon, in that time period.

MacGinitie (1937, p. 112) did an extensive study of the Weaverville beds, which he assigned to the Oligocene. The beds lie in the Klamath Range of northwestern California, clustered near the Trinity River, hemmed in between ocean and the rising mountains to the east. The difficulties inherent in the identification of fossil material are well illustrated in the case of the Weaverville *Juglans*. Diller (1911) quotes Knowlton as having made determination of *Juglans schimperi* Lx. [reinterpreted by MacGinitie (1937) to *Inga lancifolia* MacG.], *Juglans egregia* Lx. and *J. oregoniana* Lx. from the Weaverville flora. MacGinitie reassigned both of the latter specimens to *Juglans orientalis*. He characterized his expanded interpretation of *J. orientalis* MacG. as having a much closer resemblance to various living species of *Juglans* in eastern Asia than to living forms in North America. LaMotte (1936) working in the upper Cedarville flora of the northern Great Basin (east of the Cascades and north of the Sierra Nevada), transferred *Juglans oregoniana* Lx. to *Carya* with what appears to be fairly cogent argument.

During an investigation of the Pliocene San Pablo beds, Condit (1938) identified fossil leaves from those beds as *J. oregoniana* Lx., defending his identification vigorously in opposition to LaMotte's reassignment of this species to *Carya*. As far as the records of these four investigations show, the workers had leaves or leaflets only, and no fruits. But whether *Juglans* or *Carya*, the species described by MacGinitie as *J. orientalis* MacG. disappears from the North American scene, apparently unable to cope with the environmental changes of succeeding ages. No descendants are recognized in California today.

An obvious geographical unit in the western United States is that which centers in the Cascades. This mountain range, extending north-south from the Canadian border across Washington and Oregon, penetrates northern California for a brief distance, curving off toward the east and culminating at Mount Lassen, thus lying entirely north and west of the Sierra Nevada. This is an area in which extensive paleontological studies have been made. Chaney carried out investigations of the fossil floras of three Pliocene sites in the Cascades: Deschutes (1938), Dalles and Troutdale (1944 a,b); he reported no *Juglans* from his studies of the Troutdale and Dalles flora, but described a species in another genus of the same family, *Pterocarya oregoniana* Chaney. He placed it in the East Asian Element, and listed *P. stenoptera* DC. as its nearest living equivalent species. The extant *P. stenoptera*, common in parts of China, is not generically represented in North America today. Chaney's study of the Deschutes flora (1938, p. 203) disclosed no evidence of either *Juglans* or *Pterocarya*.

Axelrod first studied the Sonoma flora in 1944 and later (1950a) he issued a report on "A Sonoma Florule from Napa, California", in which he identified *Pterocarya oregoniana* Chaney. In his digest of geological history which is included in Munz and Keck's "California Flora" (1959, p. 6) Axelrod stated that *Pterocarya,* together with a few other East American and East Asian species persisted in the mild coastal strip from central California northward, becoming extinct in the early part of the Pleistocene.

The wide area east of the Cascades is rather better documented than is the area to the west. This eastern region, tenanted by plant immigrants from the holarctic forest, provided a favorable environment for the development of a significant Miocene flora. LaMotte (1936, p. 90) believed that the general outlines of North America in upper Miocene time may be considered to have been much the same as today, the physiography and the inferred climate providing conditions favorable to an extremely uniform fossil flora. He reports the finding of numerous leaflets (1936, p. 116), with at least two specimens of leaves showing leaflets in place, but identifies the entire group as *Carya egregia* Lx., feeling that the characteristics resembling hickory outweighed those resembling *Juglans*. What seems important here is not that the botanists disagree on nomenclature, but rather that the evidence for a dominant broad-leafed deciduous forest of oak-hickory-beech association thrived east of the Cascades in Miocene time, an environment that would have been favorable to the persistence of the many species of *Juglans* found in Washington, Oregon and Idaho in preceding and contemporary fossil beds. Berry's work (1927) on the flora of the Esmeralda beds convinced him that all evidence pointed to the presence of a permanent body of water in western Nevada in the Miocene.

Wolfe (1959, pp. 46, 47, 48)[1] describes two fossil *Juglans* from the Miocene: *J. hesperia* from northwestern Oregon and *J. fryi* from the northeastern part of the state. Both of these fossil forms had resemblances to *J. kentensis* referred to in the discussion of Oligocene specimens, but also exhibited what he considered to be significant morphological differences. Chaney (1927, p. 74) identified materials from eastern Oregon as *J. oregoniana* Lx., and MacGinitie (1933, p. 50) identified material from southern Oregon as the same species, but Chaney considered the nearest living equivalent to be *J. californica* Wats., whereas MacGinitie considered his specimen to be closer to *J. nigra* L.

Two more references to Miocene *Juglans* appear in the literature. The first is *J. nevadensis* Berry (1928), exact provenience unknown, but found in the desert east of Truckee. Berry believed it to have a possible affinity to *J. regia* or *J. sieboldiana* Maxim of Japan, basing such evaluation on the lack of corrugation in the shell surface. The second is from Axelrod (1950b) who in his restudy of some of the Middle Pliocene Mount Eden flora, amended his description of *J. beaumontii* Axelrod to include two species: a) *J. beaumontii* Axelrod emend. with an affinity to *J. rupestris* Engelm. of the southwest United States and b) *J. nevadensis* Berry, described as having a smooth outer shell-coat with minor surface irregularities and greatest affinity to "*J. californica* of southern California" (p. 102).

Dorf (1936) investigated the Weiser beds of southwestern Idaho. This site, east of the rising Cascades, is placed in the Upper Miocene or Lower Pliocene time. Dorf imputed a more xeric environment with a rainfall of probably less than twenty-five inches. He described *J. hesperia* Knowlton which he related to *J. nigra* L., pointing out the similarity of the inferred Weiser climate to the climate of today in the eastern United States.

It would appear, therefore, that already in Miocene time, some *Juglans* species were established on the east side of the Sierra Nevada. Chaney (1938) concluded that the northern Sierra was sufficiently high at the beginning of the Miocene to have eliminated most of the genera requiring summer rainfall. Isolated there by the rising range and cut off from ocean moisture, the conditions became increasingly xeric, and the genus faced the inevitable choices which changing environments present to the plant world: adapt to change, migrate, or become extinct.

We come now to a consideration of the third geographical unit, the

[1]*Juglans hesperia* Knowlton has been transferred to *Salix*; *Juglans hesperia* Wolfe and *J. fryi* Wolfe (as well as *J. kentensis* Wolfe) are unpublished.

great Central Valley which lies south of the Cascades, east of the Coast Range, and west of the Sierra Nevada, closed off at the south by the Tehachapi Mountains. A number of fossil localities have been studied in the Coast Range and in the western foothills of the Sierras (see distribution map, Chaney, 1944c). The Chalk Bluffs, La Porte and Oakdale beds have shown no material identified as *Juglans*, although the Chalk Bluffs flora did include specimens identified by MacGinitie (1941, p. 101) as *Carya sessilis*.

With Condit's studies of the Remington Hill and Table Mountain floras (1944a, b), we reach the southern limit of fossil *Juglans* reported within the Central Valley. The Remington Hill and Table Mountain floras occur in, to quote a favorite phrase of the early paleontologists, "the auriferous gravels of the Sierras". The Sierras of the Pliocene were yet of moderate height and the Table Mountain beds, located in a region drained by the Tertiary equivalents of the Merced and Stanislaus Rivers, may have been laid down at an elevation not more than five hundred feet above the level of a sea which lapped at the foothills—a sea which was a hundred miles or so farther inland than it is today. Condit reports that the Remington Hill beds are at an altitude of 3840 feet today, which would imp'y that they were laid down at a greater elevation than the beds of Table Mountain.

Condit (1944a, p. 42) described a fruit from the Remington Hill beds which he named *Juglans pseudomorpha* and thought might be related to *J. nigra*, but the association in the fossil flora suggested that it was intermediate between the typical eastern black walnut and the living California black walnuts, "*J. californica* of Southern California as well as *J. hindsii* of the inner north coast range bordering on the Sacramento Valley" (p. 28). Wolfe (1959, p. 49) was of the opinion that Condit's specimen is undoubtedly a *Juglans*, but that it is too badly crushed to permit comparisons.

Condit's study of the Table Mountain flora (1944b) included a renaming of Lesquereux's *Rhus typhinoides* to *Carya typhinoides*. He discussed the similarities of *Carya* and *Juglans* at length, and considered the possibility that on ecological grounds *C. typhinoides* should be assigned to *Juglans* rather than to *Carya*.

Wolfe (1959, p. 47) reassigned the Table Mountain leaflets to *Juglans*, giving them the name *J. tuolumnensis*. He was of the opinion that this fossil might have been derived through *J. hesperia* Wolfe, mentioned in the discussion of Miocene flora of northwestern Oregon, but he saw a more obvious relationship with *J. californica* Wats.

Fossil records for the Pleistocene in western North America are so sparse as to be almost non-existent. One allusion in the literature is made by Axelrod (1944, p. 118), wherein he refers to ". . . . . the occurrence of a characteristic fruit of *Juglans californica* Watson in the Pleistocene of the San Joaquin Valley (H. L. Mason, oral communication, July, 1940)". Verification of Pleistocene remains, perhaps through fossil walnut pollens from the San Joaquin Delta peats, would greatly reinforce our understanding of pre-Holocene distribution.

To summarize the fossil record:

(1) Members of the Juglandaceae, such as *Juglans orientalis* MacG. and *Pterocarya oregoniana* Chaney, which flourished in the western parts of California in the Oligocene and Pliocene, respectively, appear to have become extinct not later than early Pleistocene; as far as is known the only living equivalents are now found in Asia.

(2) The rise of the Cascades and of the Sierra Nevada in the Miocene isolated species of *Juglans* into westward and eastward slope environments; across Oregon and Idaho and down the eastward side of the Sierras there appears to have been a migration of *Juglans* tolerating more xeric conditions, the plants developing a low, bushy conformity with foliage and fruit showing tendencies toward desert-shrub.

(3) By the Pliocene there were on the west side of the Sierra Nevada several species of *Juglans* that had made the adaptation from the subtropical environments of the Eocene and were flourishing in the cooler, summer-dry climate of the Pliocene at elevations now comparable to the lower Sierra Nevada. They occurred in the vicinity of the Tertiary rivers, probably not too high above the then great inland sea which reached to the foothills of the Sierra. It does not seem to be merely a coincidence that one finds today isolated stands of great trees at an altitude of around 1500 feet, on both sides of the Central Valley.

(4) As the Pleistocene ice advanced and the temperature lowered, the waters receded and the outline of the Central Valley was indicated. Three courses were open to the flora: it could stand steadfast and become extinct, it could adapt itself to the environmental change, or it could migrate toward the south or toward the coast. It has been generally accepted that portions of the California flora migrated southward, advancing and retreating with the deterioration of the Tertiary climate. This assumption should be generally valid. Specifically, however, the record would indicate that it was not necessarily true of every genus. In the matter of *Juglans*, it would seem that there may have been a separation as early as Miocene time, with the result that *J. californica* Wats. was derived perhaps through *J. nevadensis* Berry, *J. rupestris* Engelm., *J. beaumontii* Axelrod emend., or other similar small-leaved, small-fruited species, which tolerated the more xeric environment of the southern parts of the United States, whereas the ancestors of *J. hindsii* (Jeps.) Jeps., may well have advanced coastward before the cold, following down the streams of the Central Valley, never approaching the coast beyond the edge of the fog-drip belt, retaining its mesic characters of lofty height, lush foliage, and smooth, faintly-grooved flattened nut.

It can be concluded, therefore, that the climate and physiography were such as to make possible, or even probable, the independent evolution of the southern California black walnut, *J. californica* Wats. and the northern species, *J. hindsii* (Jeps.) Jeps., neither species being derived from the other. As a corollary, if the theory of separate and indigenous species is borne out by competent botanical investigation, the "anomaly" of distribution raised so frequently in the past, does not exist; the presence of *J. hindsii* in north-central California assumes an aspect of rightness and logic, and requires no Indian trade to account for its narrow distribution in the Central Valley drainage basin and its focus in the San Francisco Bay area.

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A CONTROLLED HYBRID BETWEEN SITANION HYSTRIX AND AGROPYRON TRACHYCAULUM

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Students of evolution have become increasingly aware of the extensive hybridization that exists between genera and species in the grass family, particularly the tribe Hordeae. Probably no other family in the plant kingdom is destined to undergo such a fundamental revision of concepts of genetic relationships among genera as is occurring gradually in the Gramineae.

The present paper reports the meiotic chromosome behavior, fertility, and comparative morphology of a controlled hybrid between *Sitanion hystrix* (Nutt.) J. G. Smith and *Agropyron trachycaulum* (Link) Malte.

Materials and Methods

Specimens of *A. trachycaulum* growing in fields near Logan, Utah, and those of *Sitanion hystrix* from Mantua, Utah, were transplanted to a field nursery in 1954. The crosses were made the following year.

Forty florets involving several spikes of *S. hystrix* were hand-emasculated in June. Mature culms of *Agropyron trachycaulum* were placed in bottles of water and the bottles taped to stakes driven in the ground beside the culms of *Sitanion hystrix*. Each culm of *S. hystrix*, with its adjacent pollinators, was then covered with Kraft paper sacks.

Two seeds were harvested in early August and planted later that same month in the greenhouse. The plants grew vigorously and a few spikes were produced the following year. One plant proved simply to be a selfed